

Introduction: the diversity of taxonomies

by *Jeremy J. D. Greenwood*

Taxonomy and related fields are battle grounds onto which the non-combatant ventures at his peril, liable to be shot at from all sides. Even the definition of the subject is one on which its practitioners clearly disagree. I shall accept that: "Taxonomy is, strictly speaking, the study of the principles and practice of classification" (Jeffrey 1977). Classifications have three main uses in biology: they allow us to summarise and organise our knowledge about living organisms, they help us to identify organisms, and they can provide an approximate summary of evolutionary relationships. The first is important because of the sheer diversity of living organisms and the second because that diversity makes identification difficult. Summarising evolutionary relationships is important because "Nothing in biology makes sense except in the light of evolution" (Dobzhansky 1973). So most biologists use classifications in most of their work. One might therefore assume that taxonomy would be a key element in the education of young biologists. In Britain, at least, this assumption would be completely unjustified; without having carried out any systematic investigation, I suspect that most undergraduate courses are devoid of formal teaching in taxonomy. As a result, most of us have a rather hazy knowledge of the principles and methods underlying classifications; even worse, because we use classifications every day of our lives, we may be unaware of quite how hazy our knowledge is. Furthermore, Arthur Cain's (1959) prescient opinion that "we are about to see a considerable revision of the whole basis of taxonomic theory" has been amply justified; with the major developments in taxonomic philosophy, in sources of data, and in analytical methods that have occurred in the last four decades, the gap between the taxonomist and the users of the taxonomists' products may, indeed, be wider than ever before. For that reason, I shall take some space to look at those developments, in the hope that my brief summary may be of use to others who feel the need to be more familiar with modern ideas in taxonomy but whose work, like mine, has prevented them from closely following those ideas as they have developed. My own recent education in the subject has relied particularly on: Ridley (1986), who provides a thought-provoking, if personal, view of the major schools of taxonomy from the point of view of an evolutionary biologist rather than of a practising taxonomist; Forey *et al.* (1992), who clearly explain cladistic views and methods; and Hillis & Moritz (1990), who cover many of the principles as well as covering in detail how molecular evidence may be used. (For those whose knowledge of molecular evolution is becoming rather rusty, Li & Graur (1991) provide a useful introduction to current ideas.)

Organising knowledge

We are able to use classification as a means of organising knowledge about living organisms particularly because species fall into clusters.

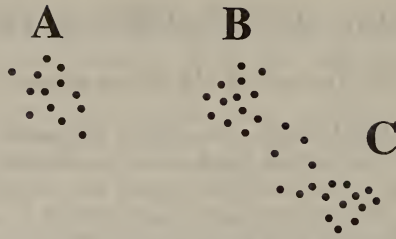


Figure 1. Clusters of species in a two-dimensional character space. Cluster A is distinct but do B and C represent one cluster or two? If they form two clusters, where should the dividing line be drawn?

For example: bird species share certain characteristics in common, mammal species share other characteristics, and there is a gap between them; bats share some characteristics with birds but are still firmly linked to the mammals by most of their characteristics; bats do not cause us to have difficulty in recognising the two chief clusters of warm-blooded vertebrates or in distinguishing between them. We can make general statements about all members of such clusters, to help us reduce our knowledge base to manageable proportions. The process is further facilitated by the fact that we may arrange the clusters in a non-overlapping hierarchy, with clusters at each taxonomic level themselves being clustered at the level above. Unfortunately, the clusters into which species tend to fall are often indistinct (Fig. 1), especially when we consider fossils as well as extant species (Fig. 2), so the distinctions between taxa may not be clear and generalisations about the members of a taxon may not all apply to every species.

Evolution: branching and divergence

For many, the chief fascination of biology is that living organisms have an evolutionary history, being related to each other through descent from common ancestors. The history of life can be described by a simple branching pattern (e.g. Fig. 2) and that pattern can be reflected by the taxonomic hierarchy. Because evolution is central to biology, taxonomy has traditionally been used to summarise evolutionary relationships as well as to provide groups (clusters) about which general statements can be made. For example, as well as being seen to have many characteristics in common, species in the class Aves are recognised as sharing an evolutionary relationship closer than the relationship between any one of them and any species in other classes.

If species that were evolutionarily closely related were always more similar than those that were more distantly related, classifications could easily reflect both degrees of similarity and degrees of relationship. Unfortunately, this would only be true if evolution involved species descended from a common ancestor simply becoming steadily more and more different from each other (Fig. 3a). Unfortunately, life is not that simple: rates of divergence vary, as in Fig. 3b, in which species 3 is now

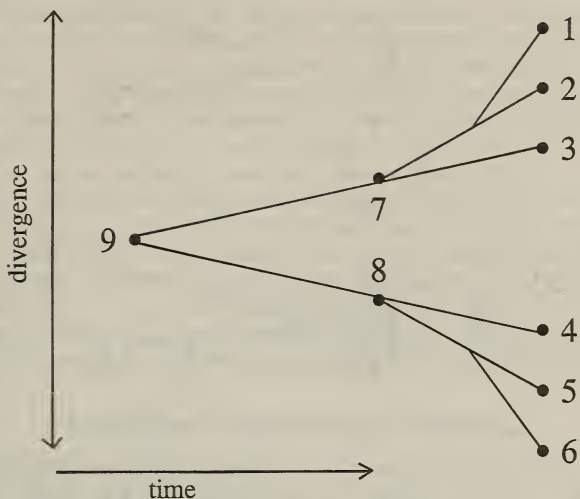


Figure 2. A hypothetical evolutionary tree in which six extant species (1–6) form two distinct clusters on the axis of divergence. The known fossils (7–9) link these clusters together.

more different from species 2 than the latter is from species 1, even though species 2 and 3 share a more recent common ancestor; convergent evolution is equally destructive of the correspondence between similarity and evolutionary relationship (Fig. 3c).

The diversity of taxonomies

Because patterns of similarity and evolutionary relationships may not be congruent and because there are various ways of describing both similarities and relationships, different taxonomists may employ different principles and procedures in their work. For the purposes of exposition, I recognise five main groups: the traditional evolutionary taxonomists, pheneticists, distance-based evolutionary taxonomists, Hennigian cladists and pattern cladists. Cladists have dominated taxonomic thinking in recent decades and some (perhaps all) of them claim that the other schools are now extinct. That this is not true is shown by the fact that the best-known recent classification of birds (Sibley & Ahlquist 1990) is distance-based. Furthermore, many non-taxonomists have grown up knowing something about traditional evolutionary taxonomy and may assume that all biological classifications rest on traditional principles and procedures. Indeed, because classifications take time to re-work, many of them still do.

It is clearly important that those who use a particular classification should know and understand the taxonomic principles used to produce it. If they do not, they are likely to draw invalid conclusions from it. The most important message I have to deliver is that it is up to the

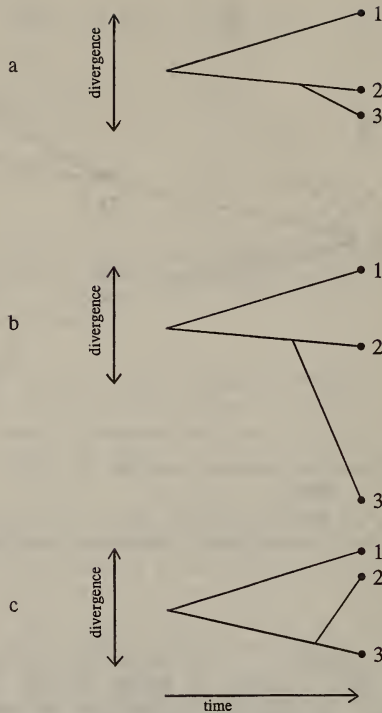


Figure 3. Three evolutionary trees. Note that each is meant to represent the actual course of evolutionary events, not what might necessarily be inferred from available evidence. In (a) species diverge at fairly steady rates, so that degrees of similarity between extant species reflect their evolutionary relationships. The correspondence between similarity and relationship is broken in (b) because rates of divergence differ and in (c) because of convergence.

taxonomist to state clearly the principles and procedures involved in producing a classification and up to the user to pay proper attention to such statements.

What sorts of characters to use?

Taxonomists differ not only in their principles and procedures but also in the sorts of characters they use as the basis for their classifications. Morphological characters have traditionally been dominant but the use of other characters has a long history: not only have naturalists long used song to identify and distinguish similar birds (e.g. White 1789) but among formal taxonomists Linnaeus (1758) used behaviour ("adscendit noctu", in respect of *Lumbricus terrestris*) and Nuttall (1904) used immunological characters. From time to time, individual taxonomists have promoted the use of particular sets of characters, either because of the ease with which they may be studied or because they are

supposed to be particularly revealing of evolutionary relationships. The latter suppositions generally rely on questionable arguments about certain sorts of characters being evolutionarily conservative because they are likely to be less (or more!) subject to natural selection than other sorts. But, just as the history of evolutionary biology is littered with examples of characters once thought to be selectively neutral but now known to be strongly selected, so is the history of taxonomy littered with classes of characters no longer thought to be peculiarly valuable. Molecular (especially DNA) data are still often thought to be especially useful but they produce no more consistent pictures of phylogeny than do morphological data (Patterson *et al.* 1993, Sheldon & Bledsoe 1993). The best classifications are likely to result from considering all the available data—though for evolutionary and cladistic taxonomies homologous characters are of particular importance.

Traditional evolutionary taxonomy

What one regards as traditional evolutionary taxonomy is a matter of opinion. I refer to the approach, growing out of “The Modern Synthesis” of Stebbins (1950), Simpson (1961) and Mayr (1969), which has been further discussed by Cronquist (1988) and Bock (1989). It involves working out the evolutionary history of the species under consideration, taking into account evidence such as ecology and biogeography as well as the distribution of characters among species. Attention is paid to the function of characters, with assessments being made of the likelihood of different possible evolutionary changes; it is important to assess whether or not similar character states are homologous or the result of convergence. This is because taxa are required to be monophyletic which means, for the traditional evolutionary taxonomist, merely that all group members should share a common ancestor, which should also be a member of the group (Fig. 4). Note that it is not necessary that all the descendants be included for a taxon to be regarded traditionally as monophyletic, so a divergent species (or group of species) can be separated from a group with which it shares common ancestry (as taxa VI and VII are separated from taxa III and IV in Fig. 4c). For the cladist (see below), in contrast, taxa III and IV (Fig. 4b and 4c) are paraphyletic (and not allowed); strict monophyly requires that all descendants are included in the group. Thus traditional evolutionary taxonomies attempt to reflect both the branching pattern of the evolutionary trees and the extent of divergences.

The problem with traditional evolutionary taxonomy is that it is highly subjective, both at the stage of working out the underlying evolutionary narrative and at the stage of converting the phylogenetic tree into a classification.

Phenetic taxonomy

Pheneticists dispense with the subjectivity of traditional evolutionary taxonomy by abandoning the attempt to summarise evolutionary relationships in the classification. For the phenetic school, taxonomy is

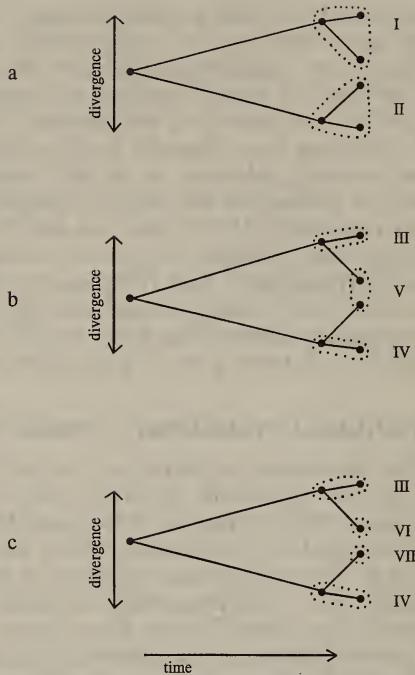


Figure 4. A hypothetical evolutionary tree and various classifications (a-c) for four extant species and two known fossils. Classification (a) would be acceptable to both traditional evolutionary taxonomists and cladists, since taxa I and II are monophyletic. Classification (b) would be more acceptable to a phenetic taxonomist, because taxon V reflects the similarity between the two species falling into it; but this taxon is polyphyletic, so the classification would be rejected by both traditional evolutionary taxonomists and cladists. The latter would also object to the paraphyletic taxa III and IV and so would also object to classification (c), though this would be acceptable to traditional evolutionary taxonomists. Whether one of the latter preferred (a) or (c) would depend on the weight he or she gave to divergence relative to phylogenetic relationship.

a matter of producing a hierarchy that reflects the inherent hierarchical clustering of nature. Species are grouped according to degrees of resemblance. In effect, species are seen as points in a multi-dimensional hyperspace, the dimensions corresponding to various characters and the positions along those dimensions being determined by how different the species are in respect of those characters. The phenetic taxonomist's job is to establish the dimensions, to measure positions and distances, and to recognise clusters (and the clusters of clusters . . .). Thus the pheneticist would apply classification (b) in Fig. 4; the fact that taxon V is polyphyletic is immaterial, since the taxa are units of resemblance not of phylogeny.

At first sight, phenetics is less subjective than traditional taxonomy because it requires no judgements about evolution. But, as Ridley (1986) and others have pointed out, it is possible to define and measure

“similarity” in a variety of ways and the choice between them is entirely arbitrary; furthermore, a large variety of different methods is available for defining clusters and the choice is again arbitrary. Because the classifications produced may differ markedly according to which similarity measures and clustering methods are used, it is difficult to argue that phenetic methods are superior to traditional methods.

Distance-based evolutionary taxonomy

The extent to which single-strand DNA from two different sources produces hybrid double strands under specified conditions depends on the extent to which the two DNAs contain identical sequences, so such hybridization provides a measure of similarity. If it were true that evolution at the level of DNA (base substitution) proceeded in a steady, undirected, clock-like manner and provided that one could properly correct for the likely occurrence of changes that limit divergence (parallel changes in the two species and multiple changes, including reversals, at single nucleotide sites), then the similarity between species would reflect their evolutionary relationship (as in Fig. 3a). An essentially phenetic classification based simply on the degree of resemblance (of DNAs) would then have an evolutionary interpretation. However, the speed at which the “molecular clock” runs is clearly far from constant (Hillis & Moritz 1990) and the corrections required for parallelism, multiple hits and reversals are based on somewhat arbitrary assumptions. Furthermore, distance measures based on DNA-DNA hybridization are subject to considerable experimental error (Werman *et al.* 1990). It is for these reasons and others that the classification of Sibley & Ahlquist (1990) aroused so much controversy (see Sheldon & Bledsoe 1993, Harshman 1994). It has, nonetheless, become widely accepted, as have other classifications based on the idea that the degree of similarity (especially of DNAs) can be used as a direct assessment of evolutionary relationships.

Hennigian cladistics

Hennig (1950, 1966) revolutionised systematics by proposing clear, non-arbitrary methods for exposing the patterns of diversity that result from phylogenetic branching and for describing those patterns in an hierarchical classification. Both Ridley (1986) and Forey *et al.* (1992) present clear introductions to cladistic methods. Forey *et al.* describe its axioms as:

1. Nature's hierarchy is discoverable and effectively represented by a branching diagram.
2. Characters change their status at different hierarchical levels. Characters within a study group that are either present in all members of the study group or have a wider distribution than the study group (plesiomorphies) cannot indicate relationships within the study group.
3. Character congruence is the decisive criterion for distinguishing homology (synapomorphy) from non-homology (homoplasy).
4. The principle of parsimony maximises character congruence.

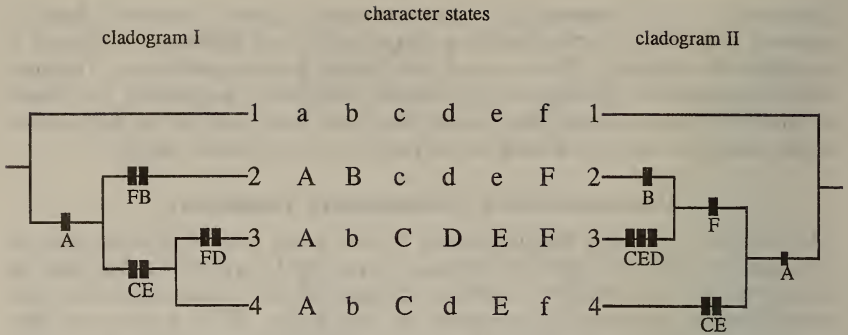


Figure 5. Two alternative cladograms for species 2, 3 and 4, based on six characters, for which the primitive states (seen in the 'outgroup' species 1) are represented by lower case letters and derived states by upper case letters. The dark bars represent points at which a primitive state changes to a derived state. Redrawn from Forey *et al.* (1992).

The branching diagrams produced by cladistic methods are referred to as cladograms. By "character congruence" is meant the co-occurrence of characters, such that they specify the same taxonomic group. Thus in cladogram I of Fig. 5, C and E are congruent (since they both occur in, and only in, the group 3-4) whereas F is incongruent with them (since it occurs not only in some, but only some, members of the group but also outside the group). Incongruencies imply convergent evolution. Cladogram II has fewer congruencies and more incongruencies than cladogram I, entailing more evolutionary changes and more convergences. By the principle of parsimony, cladogram I is preferred over cladogram II.

The stark clarity of cladistics is a recommendation in itself. Furthermore, it allows not only the process of cladogram building to be computerised but also the ready search for, and objective comparison of, alternative cladograms. Cladistics is not, however, completely objective and non-arbitrary: the taxonomist's judgment is important in defining characters and judging homology, in particular. The comparison of DNA sequences shows this up most starkly. Because sequences evolve both by substitutions of one nucleotide by another and by changes in number of nucleotides (by deletion or insertion), there are often various ways of explaining differences between homologous sequences, depending on the numbers of substitutions and deletions/insertions assumed; parsimony cannot fully resolve such cases because it is usually impossible simultaneously to minimise the number of substitutions assumed and to minimise the number of deletions and insertions.

Traditional evolutionary taxonomists have a more fundamental objection to cladistics than simply that it is not as objective in practice as it is in principle. This is that cladograms do not reflect the underlying evolutionary tree in the way that the traditionalists would like them to do. The problem lies with the cladists' rejection of paraphyletic groups, i.e. taxa which do not contain all the descendants

of the common ancestor, such as taxon III in Fig. 4. One manifestation of the problem arises from traditional classifications attempting to show patterns of divergence as well as patterns of branching whereas cladistic classifications are concerned only with branching. For example, traditionalists separate the Class Aves from the Class Reptilia because of the great divergence of birds from reptiles, whereas cladists do not allow this because birds are descendants of the common ancestor of reptiles (indeed, they are, in branching terms, more closely related to crocodiles than either is to turtles or to lizards and snakes). Which classification better represents the evolutionary tree depends on one's view of the relative importance of branching and divergence. The second manifestation of the paraphyly problem is illustrated by Fig. 5, in which species 1 shows the primitive condition for all characters. Thus, on the evidence available, the most parsimonious view of the evolution of the four species in the Figure is that species 1 is the common ancestor of all of the others. However, cladistics involves recognising groups by homologies and has no means of distinguishing ancestor-descendant relationships. (Cladists would, indeed, argue that no-one has such means since, even if species 1 was represented in the fossil record at a time compatible with its being the ancestor of the others, there is no way of knowing that the fossil specimens were certainly ancestral to the other species.) Furthermore, to recognise species 1 in Fig. 5 as the ancestor of the other species would make that species itself a paraphyletic taxon, since it does not contain all its descendants. A practical example, if one assumes *Archaeopteryx* to represent the ancestor of all later birds, is that *Archaeopteryx* cannot be recognised (in a cladistic classification) as a genus equivalent to other avian genera, because it would then be a paraphyletic taxon. Cladists have attempted to resolve this problem in various ways, though none of the solutions produce classifications that non-specialists find easy to understand. Whether the matter will be resolved by non-specialists becoming sufficiently educated to be able to understand such classifications or by the partial acceptance of paraphyletic taxa, I am reluctant to predict.

Pattern cladistics

Pattern cladistics uses cladistic methods to produce classifications but it avoids the uncertainties involved in working out phylogenetic trees and the problems that arise if one tries to describe trees through classifications by ignoring evolution (for the purposes of classification). In brief, it concentrates on the pattern of organic diversity rather than on the process that produces the pattern. Ridley (1986) has argued that, once evolution is abandoned, there is no justification for cladism (it is reduced to just one arbitrary method among many for pigeon-holing animals and plants) but pattern cladists would reply that, to study evolution, one should describe the patterns first (without preconceptions) and then worry about the processes. They remain the major force in modern taxonomy and their methods have undoubtedly been useful in many systematic and biogeographical studies.

Topics addressed in the symposium

Endler (1989), in a balanced and illuminating review, has pointed out that not only is there a variety of different species concepts but that there are several major differences in the aims of species concepts and that different concepts have different uses. Much attention at the symposium, led particularly by Liversidge, by Zink and by Snow, focused on the relative merits of various species concepts, especially the *biological* and the *phylogenetic* species concepts. The latter, though it comes in various forms (see Cracraft 1983, 1989, McKittrick & Zink 1988, Nelson 1989), can be seen as a logical extension of cladistics to the species level, with its concentration on pattern rather than process. There is no doubt that, because of uncertainties associated with assessing the 'process' (potential interbreeding), defining biological species is not always easy or objective. Indeed, most evolutionary biologists would agree with Templeton (1989) that his "cohesion species concept" is generally more useful than the traditional biological ("isolation") species concept; but this still emphasises process rather than pattern. The phylogenetic concept may appear to resolve problems by concentrating on pattern but some of us remain to be convinced that it will prove more workable in practice. Indeed, disputes over trinomials (discussed at the symposium by Violani & Barbagli) are symptomatic of the difficulties of defining taxa at levels below that of the biological species. The well-known difficulties for the biological species concept of deciding whether or not to treat allopatric forms as separate species are paralleled for the phylogenetic species concept: if one applies the usual criterion under this concept that the two populations are to be specifically separated if they are diagnosably distinct, then one would separate two populations that differed at only a single genetic locus provided that difference was consistent; this would not generally be helpful, but the alternative is to impose an arbitrary rule about how much difference is required before one treats two forms as separate species—just as when applying the biological species concept to allopatric forms.

Which species concept one uses clearly has implications beyond systematics (some being explored at the symposium by Knox and by Collar) but in my view the critical points are ones that centre on systematics itself. Firstly, even though the process of speciation is usually gradual and not always a simple branching, the stage at which the genetic and ecological cohesion of a species breaks down to produce two or more separate daughter species (themselves internally cohesive) represents an important discontinuity; the separation itself favours more rapid genetic and ecological divergence, so there is a positive feedback. Secondly, the criterion of reproductive and ecological cohesion results in biological species having an objective existence in a way that other taxonomic levels do not—"the species is not an invention of taxonomists or philosophers, but it has a reality in nature" (Mayr 1988). That is why most modern philosophers of biology reject the idea that species are classes, though they may differ as to whether they are therefore to be described as individuals (see discussions in

Mayr 1988, Hoffman 1989, Sober 1993). Admittedly, this argument falls down if, like some cladists (Nelson 1989), one does not believe in species. Such extreme views should not lead us to conclude that the ideas involved in the phylogenetic species concept have nothing to offer in terms of improving our classifications. Equally, the occasional difficulties of applying the biological species concept should not lead us to abandon it, given its proven value in ornithology over the last half century.

The symposium was not only concerned with taxonomic principles and the consequences of applying different species concepts. Mikhailov's presentation on egg-shell structures reminded us of the constant search for new characters needed to resolve taxonomic problems. We were reminded of the intimate practical connection between classification and identification by Parkin's contribution on DNA-based methods for identifying individuals and their relationships and by Russell's presentation on identifying mummified falcons, where the nature of the material required the use of characters other than those normally employed.

Taxonomy is not just a subject for the specialists but a subject of importance for all biologists. The level of attendance and liveliness of debate at the symposium confirm ornithologists' current interests in avian taxonomy and the freshness of the presentations promise continuing developments of both ideas and methods.

Acknowledgements

I thank Professor C. J. Humphries for most valuable advice on modern taxonomic literature and him and Dr A. Knox for their forthright but constructive comments on an early draft.

References:

- Bock, W. J. 1989. The homology concept: its philosophical and practical methodology. *Zoologische Beiträge, NF*, 32: 327-353.
- Cain, A. J. 1959. The post-Linnaean development of taxonomy. *Proc. Linn. Soc. London* 170: 234-244.
- Cracraft, J. 1983. Species concepts and speciation analysis. *Current Ornithology* 1: 159-187.
- Cracraft, J. 1989. Speciation and its ontology: the empirical consequences of alternative species concepts for understanding patterns and processes of differentiation. Pp. 28-59 in D. Otte & J. A. Endler (eds), *Speciation and its Consequences*. Sinauer, Sunderland, Mass.
- Cronquist, A. 1988. A botanical critique of cladism. *Botanical Review* 53: 1-52.
- Dobzhansky, T. 1973. Nothing in biology makes sense except in the light of evolution. *American Biology Teacher* 35: 125-129.
- Endler, J. A. 1989. Conceptual and other problems in speciation. Pp. 625-648 in D. Otte & J. A. Endler (eds), *Speciation and its Consequences*. Sinauer, Sunderland, Mass.
- Forey, P. L., Humphries, C. J., Kitching, I. J., Scotland, R. W., Siebert, D. J. & Williams, D. M. 1992. *Cladistics: a Practical Course in Systematics*. Clarendon Press, Oxford.
- Harshman, J. 1994. Reweaving the tapestry: what can we learn from Sibley and Ahlquist (1990)? *Auk* 111: 377-388.
- Hennig, W. 1950. *Grundzüge einer Theorie der phylogenetischen Systematik*. Deutsche Zentral Verlag, Berlin.
- Hennig, W. 1966. *Phylogenetic Systematics*. Univ. Illinois Press.

- Hillis, D. M. & Moritz, C. (eds). 1990. *Molecular Systematics*. Sinauer, Sunderland, Mass.
- Hoffman, A. 1989. *Arguments on Evolution. A Paleontologist's Perspective*. Oxford Univ. Press.
- Jeffrey, C. 1977. *Biological Nomenclature*. 2nd edn. Edward Arnold, London.
- Li, W.-H. & Graur, D. 1991. *Fundamentals of Molecular Evolution*. Sinauer, Sunderland, Mass.
- Linnaeus, C. 1758. *Systema Naturae, Part I*. 10th edn. Stockholm.
- Mayr, E. 1969. *Principles of Systematic Zoology*. McGraw Hill, New York.
- Mayr, E. 1988. *Toward a New Philosophy of Biology*. Belknap Press, Harvard University.
- McKittrick, M. C. & Zink, R. M. 1988. Species concepts in ornithology. *Condor* 90: 1-14.
- Nelson, G. J. 1989. Species and taxa: systematics and evolution. Pp. 60-81 in D. Otte & J. A. Endler (eds), *Speciation and its Consequences*. Sinauer, Sunderland, Mass.
- Nuttall, G. H. F. 1904. *Blood Immunity and Blood Relationship*. Cambridge Univ. Press.
- Patterson, C., Williams, D. M. & Humphries, C. J. 1993. Congruences between molecular and morphological phylogenies. *Ann. Rev. Ecol. Syst.* 24: 153-188.
- Ridley, M. 1986. *Evolution and Classification: the Reformation of Cladism*. Longman, London.
- Sheldon, F. H. & Bledsoe, A. H. 1993. Avian molecular systematics, 1970s to 1990s. *Ann. Rev. Ecol. Syst.* 24: 243-278.
- Sibley, C. G. & Ahlquist, J. E. 1990. *Phylogeny and Classification of Birds*. Yale Univ. Press.
- Simpson, G. G. 1961. *Principles of Animal Taxonomy*. Columbia Univ. Press.
- Sober, E. 1993. *Philosophy of Biology*. Westview Press Inc., Colorado.
- Stebbins, G. L. 1950. *Variation and Evolution in Plants*. Columbia Univ. Press.
- Templeton, A. 1989. The meaning of species and speciation: a genetic perspective. Pp. 3-27 in D. Otte & J. A. Endler (eds), *Speciation and its Consequences*. Sinauer, Sunderland, Mass.
- Werman, S. D., Springer, M. S. & Britten, R. J. 1990. Nucleic Acids I: DNA-DNA Hybridization. Pp. 204-249 in D. M. Hillis & C. Moritz (eds), *Molecular Systematics*. Sinauer, Sunderland, Mass.
- White, G. 1789. *The Natural History and Antiquities of Selborne*. Benjamin White & Son, London.

Address: Dr J. J. D. Greenwood, British Trust for Ornithology, The National Centre for Ornithology, The Nunnery, Thetford, Norfolk, IP24 2PU, U.K.